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ON THE MORPHOLOGY AND DEVELOPMENT OF A NEW CESTODE OF THE GENUS *PROTEOCEPHALUS*.* WEINLAND

[WITH FOUR PLATES.]

GEORGE R. LARUE.

Since Fuhrmann's work, *"Die Taenien der Amphibien,"* a considerable number of species have been added to the Genus *Proteocephalus,* the addition being made from the cestodes of snakes and of fishes. No further *Proteocephalus* species have been recorded from the group of Amphibia.

It is my purpose to describe in this paper the cestode *Proteocephalus filaroides,* n. sp. from *Amblystoma tigrinum* Baird. Dr. J. H. Powers of the University of Nebraska, in carrying on a series of investigations on *Amblystoma tigrinum,* found a cestode parasite occurring in considerable abundance. Some fragments were turned over to Dr. Henry B. Ward, who later interested the writer in this form. Besides the fragments collected by Dr. Powers and placed at my disposal through the kindness of Dr. Ward, specimens have been collected from *Amblystoma tigrinum* in Cherry County, Nebraska, at Crete, Neb., and at Belleville, Kan. The host is quite abundant in the region west of the Missouri river, and, since infection is almost general, the accumulation of a relatively large amount of material has been fairly easy.

Lühe (1899) gives certain reasons for retaining the name *Ichthyotaenia* suggested by Lönnberg (1894) for this group. However, since the name *Proteocephalus Weinland* (1858) has the right of priority, it should be used to denominate the genus.

Material has been killed in formol, corrosive-acetic, picro-sublimate-formol, Kleinenberg's picro-sulfuric with an equal part of 5 per cent. solution of corrosive sublimate to which 5 per cent. acetic acid has been added, and in other killing and fixing agents. Killing fluids were generally used hot, and, since the species is small and not muscular, but little contraction resulted.

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* Studies from the Zoological Laboratory, The University of Nebraska, under the direction of Henry B. Ward, No. 95.

General Appearance. When removed from the small intestine of the host the cestodes are very active, the strobila undergoing constant changes in length and breadth. The scolex passes through changes of form with great rapidity. In this respect it fully bears out its generic name. Before killing, the cestode is white, at times somewhat transparent. Pieces which have lain for a time in the rectum of the host frequently become stained yellow or even brown.

In external appearance preserved specimens are long and extremely attenuated. One notes the long, slender neck region, the long chain of proglottids which are more or less distinctly set off from one another, and the extreme length of the mature and ripe proglottids. A typical specimen yields the following measurements: Length of body, 80 mm.; number of proglottids, 112; breadth of scolex, .46 mm.; suckers in antero-posterior diameter, 0.180 mm.; length of neck, 3.4 mm. The following table gives some relative measurements.

Number of cm. from scolex.	Proglottids in cm.	Breadth.
1 (includes neck)	39	0.36 mm.
2	26	0.46 mm.
3	14	0.50 mm.
4	10	0.53 mm.
5	6	0.63 mm.
6	5	0.68 mm.
7	6	0.65 mm.
8	6	0.80 mm.

While these figures may be taken as typical, considerable variation occurs. The length may run up to 110 mm. and possibly more. The scolex measurements show the least variation, while the length and breadth of the proglottids show the greatest. During the course of some experiments the writer has taken from the aquarium jars containing *Amblystoma* many long pieces of strobila, consisting of ripe proglottids. One piece in particular measured 78 mm. in length and contained 28 empty proglottids. Another piece 50 mm. long contained 16 proglottids, of which some single proglottids measured 4 mm. by 0.75 mm.

The cestode strobila from which the stages of uterine development were taken contained about 40 proglottids, in the ripest of which were a few eggs. The posterior part of the chain was broken off. A portion of a second strobila which was broken off at either end contained 90 proglottids, in which the sex organs had attained a fair stage of development, yet no proglottids contained ripe eggs. This explains why at times 20-30 ripe proglottids may be passed in a single string. In this piece of strobila the first proglottid measured 1.012x0.478 mm., the forty-first measured 0.810x0.626 mm., and the eighty-eighth 1.012x0.478 mm.

The scolex (Fig. 9) is small; just distinguishable to the naked eye. Three scolices give the following measurements of width: 0.366 mm., 0.386 mm., 0.46 mm. Frequently no difference can be detected in the lateral and dorso-ventral diameter, but transverse sections show the lateral diameter to be greater. Grooves or furrows may or may not be seen between the suckers, according to the state of contraction. Grooves have not been seen at the tip. The apex is conical, without depression and without a fifth sucker. Neither hooks nor rostellum are present. The four suckers are quite symmetrically arranged on the broadest zone of the head. The antero-posterior diameter of the suckers varies from 0.165-0.184 mm., the lateral diameter being slightly less.

The transition of scolex to neck is gradual. The neck, which is 0.30-0.36 mm. in breadth, varies in length from 3.40 mm. to 4.04 mm.

The transition from the neck to the first proglottids is almost imperceptible. The youngest proglottids are broader than long, measuring 0.30-0.36 mm. in breadth by 0.10-0.17 mm. in length. With the growth of the proglottid the relations between the length and breadth change gradually until in sexually mature or in ripe proglottids the length much exceeds the breadth. An extreme length of 4.0 mm. by 0.75 mm. has been noted in empty ripe proglottids, while a length of 1.6 mm. x 0.8 mm. is not uncommon.

An end-proglottid of characteristic shape is found in young and in maturing cestodes. The posterior end is more or less pointed, with usually a small indentation at the tip. The end proglottid is lost with the first shedding of the ripe proglottids, and thereafter the end of the strobila may round off or may present a more or less ragged or broken appearance.

The surfaces of well extended proglottids are rarely thrown into longitudinal or transverse folds, which fact facilitates the determination of the segmentation.

HISTOLOGY AND MORPHOLOGY. In their main features the cuticula and subcuticular structures (Fig. 37) do not vary much from the current descriptions. The cuticula measures about 8.6 microns in thickness, but this measurement is not constant over the entire body. Its surface in well-preserved specimens is never ragged or broken, but may show minute serrations. Minute pores are present.

The subcuticular muscles consist, first, of a layer of circular muscle fibers lying next to the cuticula, then a layer of longitudinal fibers. Together these muscles form a layer about 8.5 microns thick. Within the muscular layer are the pyriform subcuticular cells, whose bodies lie 5-20 microns from the muscular layer.

The parenchyma (Fig. 37) is characterized by the occurrence of large spheroidal spaces, which may reach a length of 30-45 microns. These large spaces occur within the parenchyma, in both the medullary and cortical regions, the larger spaces in mature proglottids being grouped near the vitelline glands.

Fresh material treated with a solution of Sudan III in 70 per cent. alcohol reveals the presence of oil globules whose size and arrangement agree with the spaces seen in sectioned material. Osmic acid used as a check yields the characteristic test for fat globules.

An entire strobila treated with Sudan III shows the arrangement of the oil globules. In the scolex itself no oil globules are found, or, if present, are extremely small and widely scattered. In the mid-region of the neck (Fig. 23), about 0.47 mm. from the scolex tip, lies a large mass of oil globules measuring up to 20 microns in diameter. From the posterior part of the mass, which in a somewhat flattened specimen is about 0.17 mm. broad, smaller fat globules extend posteriad in two parallel bands. These bands broaden out toward the periphery of the strobila, but remain distinct for several millimeters, after which they fuse in the midfield. In this anterior region the small oil globules are not densely massed, but as the proglottid becomes older and approaches the stage of sexual maturity the globules, which are here much larger, become closely massed. This massing is apparently due more to an increase in the size of the individual globules than to an increase in number. In this region the fields about the vitellaria show denser masses of globules than the middle proglottid area. The outermost globules are quite small. These grade over into the larger globules about the vitellaria and these in turn grade over into smaller globules in the mid-region of the proglottid. These last globules, however, are not as small as are those lying outermost.

With the development of the uterus and the uterine outpocketings and the production of eggs the larger part of the fat globules in the medullary parenchyma disappears. Apparently they are used up in the rapid metabolic processes incident to egg production. However, not the whole supply of fat is used up in this process, for even those proglottids which have shed their eggs show some large oil globules in the region of the vitellaria.

In sections of *Proteocephalus Lönnbergii* Fuhr. from *Necturus maculatus* Raf. determined and studied by the writer similar large globular spaces within the parenchyma were found whose distribution agreed with that of the globular spaces within *P. filaroides.*

Sections of an undescribed *Proteocephalus species* from *Micropterus salmoides,* to which I shall refer in this article to *P. sp.,* do not show such large spaces as do either *P. filaroides* or *P. Lönnbergii* Fuhr. Since neither fresh nor formol material is at hand no tests can be made.

In looking over the literature on the subject I find only two references to oil droplets in cestodes. R. Leuckart (1879-86: 552) barely mentions the presence of oil droplets in the lateral fields of the proglottids of a human cestode, but he does not further describe their distribution, nor does he point out their significance in the nutrition of cestode tissues. Schiefferdecker (1874) describes oil droplets in *Dipylidium caninum* and in *Taenia solium.* He describes with some accuracy their distribution in the parenchyma of the proglottid, but he does not attempt to describe their distribution in the strobila. Minute fat droplets were found in the cuticula and in the subcuticular cells. The fat droplets of the parenchyma were larger and were scattered throughout the medullary and cortical parenchyma.

In a rough way I have used fresh material *(Dipylidium caninum?)* as a check upon *P. filaroides,* and I have demonstrated the presence of oil globules therein, but I have not attempted to work out their distribution accurately in the strobila or in the proglot-

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1. This form may prove to be *Proteocephalus ambloplitis* Leidy, which it very much resembles.

tid. Thus far in all my work I have not found oil droplets in the cuticula and seldom in the subcuticula, except when they were in the act of being forced out of the proglottid by pressure.

Sections of *Taenia serrata* (?) show infrequent globular spaces 10-14 microns in diameter in both medullary and cortical parenchyma. These spaces, which were undoubtedly left vacant by the dissolved oil globules, are most numerous in the cortical parenchyma of the lateral fields.

So far as I have been able to learn no one else has described oil droplets in cestodes, this in spite of the many investigations on their finer anatomy. No one hitherto has found oil droplets in the *Proteocephalidae,* nor has anyone hitherto shown the distribution of oil droplets in the strobila of any cestode, so far as I know. Von Linstow (1891) has described large parenchyma spaces in *Proteocephalus longicollis* Rud., but he does not attempt to interpret them; they are probably the spaces left vacant by these oil globules.

Blochmann (1896) and Young (1908) describe the subcuticula and parenchyma and show their intimate relationships with the cuticula. Neither investigator notes the presence of oil droplets or the spaces where they occur.

From our knowledge of these structures we must consider the cuticula to be a membrane through which the foods in solution pass. Then the subcuticular cells and the processes of the parenchyma which extend out to the cuticula absorb these foods (Young 1908). No attempt need now be made to explain the nature of absorption. Here synthesis takes place and these products are then stored in the parenchyma spaces throughout the proglottid.

I shall not undertake an extended discussion of Schiefferdecker's theory of fat absorption from the intestinal contents of the host. His theory supposes the physical capture of food particles by subcuticular cell processes thrust out through pores in the cuticula. He found his confirmation in the now discredited theory of Thanhoffer.[2] Studies on assimilation in cestodes are now under way and in that connection I shall further consider Schiefferdecker's theory.

Chalk bodies occur in the parenchyma which agree in general with those described from other *Proteocephalus* species.

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2. Thanhoffer, L. von: "Beiträge zur Fettresorption und histologischen Struktur der Dünndarmzotten," in Pflüger's Archiv. f. d. ges. Physiol., Vol. VIII; 391.

MUSCULATURE OF SCOLEX AND STROBILA. The musculature of the scolex is fairly complex. As seen in a series of transverse sections the muscles are arranged as follows: At a depth of about 20 microns from the tip, general oblique muscles (Figs. 13 and 14) appear, which course from the right and left lateral surfaces to the dorsal and ventral surfaces respectively forming a rhomboid of muscle fibers. This rhomboid of fibers is encountered in the deeper sections until their course is interrupted or diverted by the increasing size and prominence of the muscular walls of the suckers which begin to appear at different levels from 60-100 microns from the apex of the scolex. At places the fibers (Fig. 15) appear to be attached to the sucker wall. The tangentially cut ends of these fibers may be seen even down to a depth of 200 microns from the scolex tip.

Beginning at a level of about 30 microns from the apex of the scolex and persisting at successive levels to the posterior edge of the suckers may be found a system of dorso-ventral and of transverse (lateral) muscle fibers. Thus a muscle cross (Fig. 14) is formed within the rhomboid of fibers. The fibers of the muscle cross are most numerous between the levels of 40-90 microns from the apex; thereafter their number diminishes, but the individual fibers are stronger.

With the appearance of the suckers in the series we find a diagonal muscle cross (Fig. 16), whose fibers connect opposing structures. Each muscle bundle is closely compacted in the middle, from which point it begins to flare out broadly toward either end, giving a broad attachment on the sucker wall.

To summarize the musculature of the scolex as seen in the transverse sections, we have, in order of appearance from the tip, first, the rhomboid of muscles; second, the transverse muscle cross; third, the diagonal muscle cross, the last two forming the so-called muscle star ("Muskelsterne," Riggenbach, 1896).

Lühe (1894) found no rhomboid of muscle fibers in the scolex of *Anoplocephala perfoliata.* The muscle relationships in the anterior part of the scolex were not similar to those in *P. filaroides.* In the region of the suckers he found the transverse and diagonal muscle crosses as we have it in *P. filaroides,* but much more strongly developed. The muscle relationships posterior to the suckers are again unlike those in *P. filaroides.*

Passing beyond the suckers the muscles immediately take on the arrangement of the muscles of the neck and of the younger proglottids. In this respect this cestode differs from *P. fossata* Riggenbach in that it does not possess a muscle cross posterior to the suckers. Fuhrmann (1895) diagrams the scolex musculature of *Nematotaenia dispar* Goeze, but the diagram does not agree in all respects with the musculature of this form. This furnishes additional evidence that *Proteocephalus* and *Nematotaenia* belong to distinct groups of cestodes.

A study of longitudinal sections through the scolex confirms the interpretation of the diagonal muscle-cross. Moreover, such sections give the best idea of the longitudinal muscles, which in general are heavier than the transverse fibers. Sections through the middle areas of the scolex show long fibers (Fig. 17) extending almost to the tip and terminating at either side of the median line. A vertical muscle-cross connecting the anterior part of one sucker wall with the posterior part of the wall of the adjacent sucker, and vice versa, may be made out (Fig. 18). This structure is fairly well developed. Strong, heavy, longitudinal muscle fibers continuing the longitudinal muscle system of the body pass from the neck into the base of the scolex as isolated fibers or, more infrequently, as small bundles (Figs. 17, 18). Here they find their attachment at various levels of the lower half of the suckers. A few of these fibers are attached anterior to the middle region of the sucker. The arrangement of the longitudinal muscles of the scolex agrees quite well with Riggenbach's description of *P. fossata* Rigg.

In marked contrast to the heavy musculature of the strobila in the fleshy *Proteocephalus* species, such as *P. ambloplites* and *P. torulosa,* is the extremely weak development of strobilar musculature in *P. filaroides.* Dorso-ventral and lateral muscles are present, but are weakly developed. In place of strong bands or plates of longitudinal muscles, delimiting the cortical from the medullary parenchyma, there are quite isolated fibers of comparatively small size. Even in contracted proglottids the longitudinal muscles do not present the appearance of being strong and closely set.

ORGANS OF THE SCOLEX. Reverting now to the structure of the organs of the scolex we find that the unarmed suckers, four in number, do not differ in their histological detail from those of other *Proteocephalus* species. There is no terminal sucker or depression.

However, just below the cuticula at this point lies an organ (Figs. 13 and 17), the structure of which has not yet been worked out. The organ has a length of about 63 microns and a breadth of about 34 microns, a matter of some individual variation. That this is not a thickening of the tissues of this point is attested by the fact that it lies within a narrow, clear zone which separates it effectually from the surrounding parenchyma. Apparently it is not a low-lying sucker or an invaginated rostellum, for no exterior opening could be observed. The histology of this organ has not yet been worked out, but will be undertaken in connection with the morphology, histology, and histogenesis of the plerocercoid of this cestode, a study which is now under way.

In this connection it might be said that in the plerocercoid (Figs. 4, 5, 6) this organ may be seen with great distinctness, being much larger than in the adult. In the plerocercoid occurring in the black bass *Micropterus dolomieu* Lac.) of Pelican Lake, Minnesota, this organ finds a very strong development. Unfortunately no adult specimens of this form are at hand, so no comparison of this organ in the plercercus and in the adult could be made. The plerocercoid is apparently the young form of a *Proteocephalus* species.

Riggenbach (1896) found a plerocercoid with a large terminal organ embedded in the scolex of *Corallobothrium lobosum.* From its appearance the scolex, I think, belongs to a *Proteocephalus* species. Of this Riggenbach writes: "Sein Scheitel besteht aus einem längsovalen Körper der aus homogener oder fein granulirter Substanz zu besetzen scheint. Vielleicht haben wir in diesem gebilde die Anlage eines Rostellums zu sehen."

Thus far this end organ has been found only in those species which are devoid of a terminal sucker and of a rostellum. It is found in *P. ambloplitis* Leidy, where it is figured by Benedict (1900). *P. sp.* shows it also. *P. Lönnbergii* studied by the writer shows a similar structure, much smaller, however, than in *P. ambloplitis* or in *P. sp.* Riggenbach figures no such organ for *P. fossata* Rigg., which has a terminal depression, but no terminal sucker, nor does he figure it for *P. abscisa* Rigg., which is without terminal depression or sucking disk. A new species which I shall describe in detail later has been studied. It has a fifth sucker, but this organ is not present. With the discovery in snakes of a series of new *Proteocephalus* species having either a rudimentary or functional rostellum, with or without hooks, comes an added interest in the scolex relationships. Unfortunately, the writer has not been able to examine slides of these interesting forms and must rely on the figures and descriptions of others. That such an organ, especially if it be small, may be overlooked is attested by the fact that it has been overlooked in *P. Lönnbergii* Fuhr. until discovered by the writer. A careful survey of the members of the entire genus would doubtless yield some extremely interesting facts that perhaps would throw some light upon the relationships of this genus which is so widely distributed both geographically and in regard to hosts.

Furthermore, it would be of interest to find out whether we have here to do with a cestode structure common to many unarmed species in different genera or whether it be a structure found only in this one genus and in members which are found only in North America. Apparently it has never been described in species occurring outside of North America.

Thus far no attempt has been made to assign a function or an origin to this organ. A solution of the question of origin would probably throw light upon the question of function. After all we may be compelled to adopt the dictum of Lühe (1894) that the fifth sucker is but a modified rostellum; and we may find that we have to do in this organ with a modified fifth sucker or a much modified rostellum.

NERVOUS SYSTEM. The nerve ring (Fig. 15) occurs at a depth of about 70-80 microns from the tip of the scolex. In longitudinal sections this ring may be seen at about the level of the anterior sucker edge (Fig. 17). The structure is somewhat octagonal in shape, measuring about 35-40 microns in breadth by 50-55 microns in length. At its corners nerve processes extend out toward the suckers and in some cases appear to reach them.

In the strobila the main pair of lateral nerve trunks may be observed in either longitudinal or transverse sections (Fig. 37) or in toto mounts (Fig. 2). No accessory nerve trunks have been made out. The main nerve trunk passes dorsal to the cirrus and vagina (Fig. 11).

EXCRETORY SYSTEM. The excretory system in the scolex shows a complex system of anastomosing and coiling ducts. Thence two pairs of lateral excretory ducts, remaining always within the medullary parenchyma, take a slightly sinuous course posteriad well within the paired vitellaria (Fig. 2). In the region of the cirrus-sheath (Fig. 11) the ventral duct passes below and the dorsal duct above the cirrus and vagina, and in the ovarial region (Fig. 19) they pass dorsal and ventral to the ovaries. Here the ventral vessels pass between the ovaries and the paired vitelline ducts. In this region also may be seen the ventral transverse anastomosis. It seems that a dorsal transverse anastomosis may also exist.

No anastomoses connecting the dorsal and ventral vessels have yet been demonstrated. The ventral vessel is usually more expanded than the dorsal, hence its wall appears thinner. Histologically they seem to be alike.

At regular intervals branching or simple anastomoses (Fig. 10) arise from either ventral or dorsal vessels, being more numerous from the ventral vessel in the posterior part of the proglottid. These anastomoses proceed to the ventral and dorsal surfaces. At times the anastomosis expands into a little bladder in the region of the subcuticular structures, then its lumen contracts sharply and it passes to the exterior as a small canal in the cuticula. Benedict (1900) has shown very similar structures in *P. amblopIitis*. I have seen them in both of my new forms and in *P. Lönnbergii.*

From the fact that these anastomoses to the exterior are secondary excretory openings they are called "foramina secundaria." However, there exists a wide variation in the types of structures which are grouped under this name. The "foramina secundaria" described by Kraemer (1892) for *P. ocellata* and *P. torulosa,* and by Riggenbach (1896) for *P. fossata, P. abscisa* and *Corallobothrium lobosum,* are muscular pulsatile vesicles which open at the posterior lateral margin of each proglottid. Benedict (1900) finds no such vesicles for either *P. ambloplitis* or for *P. ocellata,* nor do any of the secondary excretory openings seen by me come under the type described by Kraemer and Riggenbach.

The flame cells may be easily made out in the region contiguous to the dorsal and ventral excretory vessels. These may form little fan-shaped groups whose collecting tubules come together to form larger tubules, which later fuse with other tubules, and these in turn empty into the main ducts. Many small groups of flame cells empty directly into the main vessels by means of a common duct.

A fairly careful study has shown almost no flame cells in the cortical parenchyma, nor are they found in the midfield of the proglottid. They are relatively less frequent in the posterior part of the proglottid about the ovaries and they are not present in the inter-ovarial space. A sketch (Fig. 10) indicates approximately the area of their most frequent occurrence.

On the distribution of flame cells Braun (1894-1900) yields the following data: Schiefferdecker (1874) found them thickest between the transverse musculature of the proglottid; Hamann (1885) in *Taenia litterata* almost always only within the transverse musculature, very seldom in the peripheral parenchyma. On the contrary, Pintner (1881) and Zschokke (1888) reported that the flame cells lie thickest right here—i. e., in the peripheral parenchyma—and only a few penetrated into the tissue lying within; they especially accompanied the fibrils of the larger muscle fibers. In living animals they may be seen most numerously in the head and in the posterior proglottid, but are here less numerous. In *Bothriocephalus punctatus* Fraipont (1880, 1881) found them in like manner superficial; in *Taenia echinococcus* especially at the posterior end and in the scolex of *Tetrarhynchus tenuis* in the head, as well as in the posterior end irregularly arranged, while, on the contrary, in the neck, in the summit of the proboscis sheath and in the probosces there was a regular arrangement. Zernecke (1895) saw the majority of flame cells in *Ligula* in the region of the outer excretory plexus, also between the subcuticula and the longitudinal musculature; a number are also found between the last, also singly even in the medullary layer.

Proteocephalus Lönnbergii Fuhrmann shows the same regional relationships of the flame cells as does *P. filaroides*. *P. sp.* shows a like arrangement. No other *Proteocephalus* species have been investigated on this point.

GENITAL SYSTEM. In a general way the genitalia of *P. filaroides* (Figs. 1, 2, 3) agree with the type of genital system for the genus. Cirrus and vagina have a common lateral genital sinus. The uterus is a median ventral tube in its early stages; later it has 25-35 lateral out-pocketings on either side. The vitellaria are in the lateral fields and run the length of the proglottid. The ovary is bilobed, and is located at the posterior end of the proglottid. Behind it is the shell gland and oötype. An oöcapt (Schluck-apparat) is present. The testes are numerous, lying in two fields between the vitellaria.

In very young proglottids no sign of genitalia is visible, but in the region of the second centimeter the anlage of the genitalia may be seen in toto mounts as a longitudinal median darkly staining mass of nuclei which extends from the posterior end of the proglottid anteriad. Near the anterior end of the proglottid this dark streak turns toward the lateral surface. Riggenbach (1896) gives a good description of the early appearance of the developing genitalia.

The common lateral genital sinus alternates irregularly from right to left in the strobila. It is situated within the anterior fifth of the proglottid, and is not marked by a papilla. The vagina opens anterior to the cirrus.

MALE ORGANS. The testes, which number from 70-114, measure up to 50-60 microns in diameter. In nearly mature proglottids they are almost spherical, but with their further development they come to be polygonal on account of pressure of one on another. They lie between the vitellaria on either side of a free median zone extending back to the ovarial space. At the extreme anterior end there is a tendency for the two groups of testes to fuse (Fig. 2). In ripe proglottids they are pressed closely against the vitellaria by reason of the swollen condition of the uterus and its lateral pouches.

Each testis is covered with a delicate nucleated membrane, the tunica propria, which is continuous with the walls of a minute vas deferens of essentially the same structure. The vasa efferentia lie in a plane dorsal to the testes. These ducts fuse to form larger vessels (Figs. 1, 21), which are irregularly connected by cross anastomoses. The larger vessels finally converge to join the larger vas deferens. The vas deferens arises at a point on the inner dorsal surface of the dermo-muscular sac near the midfield and at about the end of the anterior third of the proglottid. Thence the vas deferens (Fig. 1) makes a few coils in its course anterial to the cirrus sheath. In mature proglottids the lumen of the vas deferens is small. Its walls are made up of a thick nucleated membrane surrounded by epithelial cells. A little later the testes begin to discharge their spermatozoa and the vasa efferentia are distended. These pour their contents into the vas deferens, whose walls dilate greatly, and become extremely thin (Fig. 20). The nuclei of both the inner membrane and the epithelial layer become widely separated. Only the upper end of the vas deferens retains approximately its original size and structure (Fig. 22).

In one specimen observed the vas deferens near the cirrus was greatly enlarged before any spermatozoa were present. This fact is difficult to account for, but it does not seem to point to a specific difference. It may have been an abnormality.

Entering the cirrus sheath the vas deferens enlarges somewhat and now may be called the *ductus ejaculatorius*. The ductus (Fig. 2) extends from a fourth to a half the length of the cirrus sheath, then it doubles back on itself almost to the proximal end of the sheath, where it is gradually transformed into the cirrus. The course of the cirrus is then direct to its distal end where its tissues pass over into the muscular wall of the cirrus sheath. Hence when protrusion occurs the cirrus is evaginated.

The cirrus (Fig. 25) is lined by cuticula, which is continuous with that covering the proglottid. Lying next to the cuticula is a heavy layer of circular muscle fibers, and outside of the circular muscles is a layer of more weakly developed longitudinal muscles. Then an epithelial layer follows. Prostate gland cells are numerous on the ductus ejaculatorius and on the cirrus. No retractor muscles could be demonstrated. The space between the cirrus and cirrus sheath is filled with a fibrous parenchyma.

The protruding cirrus (Fig. 35) may be frequently seen in ripe proglottids as a cylindrical fleshy organ, blunt at the tip. There is no evagination of the cirrus pouch as observed by Schwarz (1908) in *P. Marenzelleri* Barrois.

The cirrus sheath (Fig. 25) is a thin walled muscular sac, whose tissues are continuous with those of the cirrus at the distal end. Its length is about 0.22 mm., its breadth about 0.11 mm., being broadest in the posterior or proximal half. The musculature consists of weak circular and longitudinal fibers, the circular fibers lying within the longitudinal. A thin epithelial membrane forms the outermost layer. At infrequent intervals are gland cells.

FEMALE ORGANS. The vagina (Fig. 2) lies anterior to the cirrus. From its opening into the common genital sinus it describes a gentle curve to the midfield of the proglottid, then it passes directly back to the interovarial space. It lies dorsal to the median uterus. The size of the vagina varies greatly in different proglottids, being much larger when distended with semen. This distension may extend along the whole course of the vagina, or it may be confined more to the upper and the lower stretches, the middle part being more nearly normal in size. The broadened posterior part may be called a receptaculum seminis (Fig. 3). It lies just within the inter-ovarial space. Its posterior end is closely constricted to form a sort of valve.

The cuticula-like lining of the vagina, which seems to be continuous with the external cuticula, extends the full length of the organ to the end of the receptaculum seminis. It is by no means certain that this lining is a cuticula; it may be a delicate epithelium. In *P. Ambloplitis, P. sp.* and *P. ocellata* it bears cilia. Surrounding this lining is a layer of epithelial cells with occasional gland cells, which are greatly increased in number and in size in the upper dilated portion of the vagina (Fig. 25). In this region is a thin layer of circular muscles. Near the opening into the genital atrium is a weakly developed sphincter. The middle part of the vagina is lined by a cuticula-like layer, about which are muscular elements, whose nature could not be determined. The outermost layer is composed of epithelium and gland cells. The structure of the lower vagina will be taken up later.

THE ORGANS OF THE INTER-OVARIAL SPACE. The organs of the inter-ovarial space (Fig. 3) are arranged on the general plan of the members of the genus. The ovaries are connected by a mid-piece which discharges the ova into the oviduct through the oöcapt. The oviduct passes backward in a sinuous course to the post-ovarial space, then it turns anteriad and passes over to the oötype. About midway in its course the oviduct receives the vagina, which enters the inter-ovarial space from the dorsal side. Lying ventral to the ovaries and at about the level of the oöcapt are the paired vitelline ducts. These unite to form a single vitelline duct, which may become distended to form a vitelline reservoir. The vitelline reservoir passes posteriad to the oötype, which it enters at the beginning of the shell gland. The oötype is surrounded by the shell gland, the individual cells of which empty into it by means of little tubules. The oötype leads directly into an uterine passage, which passes more or less directly anteriad to a point some little distance anterior to the posterior end of the uterus. It now discharges into the dorsal side of the uterus.

This uterine passage persists as a narrow passage and does not dilate with ova, nor does it form out-pocketings along its course. Hence it certainly should be distinguished from the uterus proper and it is manifestly wrong to call the passage an oviduct. The name oviduct should be retained for the passage between the oöcapt and the oötype. Furthermore the vagina discharges into the oviduct, and not the reverse, as Kraemer (1892) has it. This point is determined by the histological structure of the organs.

While in general the relationships of the organs of the interovarial space are as described and as delineated (Fig. 3), some variations in this plan occur. The vitelline reservoir may lie on either the right or left side of this space. The courses of the oviduct and of the vagina are not rigidly followed. The state of contraction of the proglottid has much to do with the relaxed or contracted condition of the coils of these organs.

Taking up now the histology of the organs in the inter-ovarial region: That part of the vagina (Figs. 26, 39) extending from the valve of the receptaculum seminis to the oviduct is composed of a layer of cubical epithelial cells, surrounding which is a layer of muscles, the nature of which could not be determined. Then follows a layer of epithelial cells which may have a glandular nature.

The oöcapt (Figs. 24, 38) is a muscular organ lined with a thin epithelium and richly supplied with gland cells, whose cell processes can be traced well into the muscular walls. No boundary epithelium could be discovered.

The oviduct (Fig. 24) is lined with ciliated cubical epithelium, surrounding which is a muscular coat, apparently composed of both circular and longitudinal fibers. Then a layer of epithelium with scattered gland cells envelops the whole.

The oötype (Fig. 40) seems to be a development of a portion of the oviduct, for its structure is essentially the same. So far as could be ascertained, its cubical epithelium bore no cilia. Its muscular walls are more heavily developed than the walls of the oviduct. It possesses a continuation of the oviduct's external epithelium. The new element is the large mass of single club-shaped gland cells composing the shell gland. The long slender cell processes of these cells can be traced well into the muscular layers. The shell gland covers an area about 63 microns in diameter.

The uterine passage is composed of a layer of epithelial cells, whose nuclei are quite numerous. A muscular coat can not be made out. Enveloping the entire organ is a layer of superficial epithelium.

The paired vitelline ducts (Fig. 36) are composed of a single layer of flattened epithelium cells, whose nuclei appear as scattered bodies on the surface. It seems that these cells have contractile elements, for the wall has a fibrous appearance. The fibers run lengthwise of the ducts. At the junction of the vitelline ducts a new layer or lining of cubical epithelium is found extending throughout the course of the vitelline reservoir. The presence of muscle fibers could not be demonstrated.

THE VITELLARIA AND OVARIES. The vitellaria themselves (Fig. 2) are long, lateral-lying masses of follicles, grouped about an axial duct, of the same structure as the paired ducts with which they are continuous. The vitelline cells are large, deeply staining, spherical or ovoidal cells, with prominent nuclei and nucleoli. In them oil globules abound.

The bilobed ovaries are long wing-like bodies connected at the middle by a mid-piece. They are made up of branching and anastomosing swollen tube-like bodies. The margins of the ovaries are entire. The external covering is a delicate nucleated epithelium. The ova are large ovoidal or somewhat polygonal cells with prominent nuclei and nucleoli. They stain deeply.

THE UTERUS AND ITS DEVELOPMENT. The early development of the uterus, and especially the development of the outpocketings in this genus as *preformed* organs, was first correctly described by Schneider (1904) for *P. percae* Müller. His account is extremely brief, but his conception is correct. He says: "Der Längskanal des Uterus ist bereits angelegt und hat ein weites Lumen, lange bevor die Production der ersten reifen Eier eintritt. Er verläuft an der ventralen Seite als ein Kanal von kreisförmigem Querschnitt, der bereits auf beiden Seiten Ausläufer (Uterusäste) auszusenden beginnt." This view was not held by the investigators on this subject before Schneider. They considered that the outpocketings were caused by the breaking down of the uterine walls on account of the pressure of the contained eggs.

My own observations bear out Schneider's statement completely, and, since the process deserves more complete treatment than he gives, I shall outline the process of development of the uterus (Figs. 30, 31, 32, 33, 34, 35) and its outpocketings as it was observed in eleven consecutive proglottids. The drawings are camera outlines made from a toto preparation mounted in cedar oil. Later these drawings were carefully compared with frontal and transverse sections to insure correctness of detail. For convenience I have numbered the proglottids serially (1-11), beginning with the one a part of whose uterus is delineated in Figure 30.

As the proglottid approaches maturity the uterus may be observed as a small organ traversing almost the length of the proglottid. It is a slender tube of epithelial cells, whose nuclei are closely massed and whose cell bodies stain more deeply than do those of the surrounding parenchyma. At a stage in the proglottid history, when a few sperms have accumulated in the vas deferens, but none of which have yet been passed into the vagina, the uterus begins to take on the appearance shown in Figure 30. It will be noticed that at irregular intervals the epithelial cells of the uterine wall are massed together. While leading out into the parenchyma from these masses are strands of nuclei closely packed in a single row. This effect can also be seen in the preceding proglottids, but not so markedly. In them the strands of nuclei are not as long as they are here. Proglottid 2 shows but little advance in this structure; if anything the nuclei in the strands are a little more numerous, the strands a little longer.

Proglottid 3 shows sperms in the vas deferens. The vagina is dilating, but there are no sperms in it. The lumen of the uterus (Fig. 31) is of about the same size as in Figure 30. We now see that the nuclei of the strands have increased greatly in numbers, though at the tips of the strands the nuclei form a single line. Passing over proglottids 4 and 5 as showing gradual advances in development, the following one, 6, shows some marked changes over proglottid 3. Here the lumen of the uterus (Fig. 36) has increased in size. At the bases of the strands of nuclei the cells have moved apart and a lumen appears. The outer ends of the strand remain solid and taper out to single strings of nuclei. Branches appear on these strands. We have here the first definite appearance of the lateral out-pocketings of the uterus. In this proglottid no eggs were present, indeed no sperms had yet entered the dilated vagina. Proglottid 8 shows the vas deferens full of sperms, but the much dilated vagina empty. The lumen of the uterus (Fig. 33) is much larger; the lateral out-pocketings are longer and have a greater volume. From their tips the double and single strands of nuclei may be traced well into the parenchyma.

Proglottid 9 shows the vagina containing sperms throughout its entire length, while many sperms remain in the vas deferens. A very few eggs are to be seen ~~in the median~~ uterus tube. Plainly, then, the out-pocketings of the uterus are not due to the pressure of the contained ova, rather they are preformed organs.

Proglottid 10 shows a few more eggs in the anterior part of the uterus. Figure 34 shows the extreme anterior end of the uterus of proglottid 11. Here a number of eggs are seen in the lateral pockets. They are not yet sufficiently numerous to cause dilation of the uterus. In this figure the nuclei of the uterine wall, as well as those of the lateral strands, have been omitted. The latter could still be distinctly traced.

Unfortunately the strobila was broken off here and the posterior part was missing; hence the drawing of the ripe proglottid (Fig. 35) has been made from a different worm. It will be noticed here that the lateral pouches have been so dilated that their walls lie upon each other until we have the appearance of septa. This extreme dilation of the uterine pouches, and, in fact, the expansion of the uterine pouches in all stages, is apparently due to the absorption, the breaking down, of the parenchyma and the food material stored within the parenchyma as fats. These materials are probably used up in the metabolic processes incident to egg formation.

The method of discharging the eggs has received some attention by investigators of *Proteocephalus* species, who, with the exception of Schneider, described the process as a thinning of the body wall in the mid-ventral line. Into this space the eggs are crowded until, with the further growth of the uterus and with development of the eggs, the body wall becomes thinner and thinner, until it breaks apart and a cleft is formed. Pressure upon the wall of the uterus at this point causes a rupture and the eggs escape. Thus we have a *locus minoris resistentiae* developed.

However, the process is not so simple as the above description indicates. The *locus minoris resistentiae*, or, rather, the series of *loci minoris resistentiae,* are formed by a process very similar to, and simultaneous with, the development of the lateral outpocketings. At various levels in the uterus occur outpocketings, which are directed ventrally between certain pairs of longitudinal muscles. Such an outpocketing is shown in Figure 29. Here a sharp point is seen to be directed toward the cuticula. A more frequent appearance of the ventral outpocketing is shown in Figure 27, while Figure 28 delineates a condition of the uterus in the section adjoining the one from which Figure 27 was drawn. All three figures were taken from the uterus in the anterior part of the same proglottid. At least 10-12 separate regions similar to Figure 27 may be found in the same proglottid, while regions similar to Figure 29 occur more rarely.

In this condition the ventral diverticula remain for some time, then as the uterus fills the eggs are crowded out into the ventral diverticula, as well as into the lateral ones. With increasing pressure of contained eggs in the ripe proglottid, and probably with a further absorption of tissue materials in the region of the ventral diverticula, the points on the ventral wall, already undermined by the ventral outpocketings, give way, and the ventral wall now splits throughout its length in a definite line, much as a perforated piece of paper, when torn, follows the line of perforations. Thus the eggs are discharged.

It should be noted here that, since *P. filaroides* is not a fleshy form, the ventral diverticula are necessarily small. In *P. sp.* the ventral diverticula are much better developed. Indeed they pass out between the median pair of strong longitudinal muscles and there, in the cortical parenchyma, they expand into spheroidal spaces, which finally come to hold eggs. In this case not so many ventral outpocketings are formed, there being three to five. But since the proglottid is much shorter than in *P. filaroides* a large number of ventral diverticula are not necessary to produce the weakened wall. Again in the salamander tapeworm we have 25-35 lateral outpocketings on each side and in the other species but 10-16. There seems to be a correlation between the number of ventral and lateral outpocketings.

It is a singular fact that no outpocketings proceed toward the dorsal wall in either species observed by the writer. It is true that in Benedict's (1900) description the splitting of the uterus occurs on the dorsal surface, but an examination of his figures and descriptions shows an error in orientation and that the species *P. amblopitis* and *P. ocellata* described by him follow the rule of the genus. That no dorsal diverticula occur bespeaks a directive force which is difficult, if not impossible, to explain. Schneider (1904) attempts an explanation by making the single ventral outpocketing or "Spitze" of *P. percae* homologous with the preformed ventral uterus opening of *Bothriotaenia,* which is held to be homologous with that of *Bothriocephalus.* Whether any such homology between the uterus openings in *Proteocephalus* and *Bothriocephalus* exists is difficult of determination and cannot now be settled. A further comparative study of the species of *Bothriocephalus,* the *Bothriotaenia,* and the *Proteocephalus* must be made before the homology can be pressed.

Judging, however, from Schneider's drawings of *Bothriotaenia rugosa* it is thinkable that its ventral uterus opening arises in a manner similar to that in *Proteocephalus.* The fact that a single ventral uterus outpocketing is found in *P. percae,* while several occur in some of the members of the genus, does not argue against an homology, for a serial homology is possible.

In *P. filaroides* the discharge of the eggs may be accomplished while the strobila is yet intact. More frequently, however, a number of ripe proglottids break loose from the chain and pass to the exterior per anum. The majority of the proglottids have begun the act of discharging the eggs before they reach the exterior. In this way, when experimental hosts have been well fed on liver, large pieces of cestodes, consisting of 10-28 empty or nearly empty proglottids and measuring up to 78 mm. in length, have been passed. The feces of such hosts frequently contain large quantities of free eggs.

THE EGG. When discharged from the uterus the egg (Fig. 12) is covered with three membranes. The outer mucilaginous membrane is very thin and transparent. In diameter it measures from 35-100 microns, every possible gradation between these two measurements being represented. If all *Proteocephalus* species show similar variations in the measurements of the outer egg membranes this measurement is of little value. The second membrane or egg shell is hyaline, but heavier than the first. It measures from 30-31 microns in diameter, a fairly constant measurement. The third membrane is a delicate hyaline, flexible membrane, just enclosing the six hooked embryo or *oncosphere* which is developed in the uterus. Between the second and third membranes is a granular mass.

The oncosphere, which may be removed from the egg by careful pressure manipulation on the cover-glass, measures about 21 microns in diameter. This measurement shows no great variation. It is still surrounded by the closely investing third membrane. The three pairs of hooks which were somewhat obscured before now show up distinctly. In oncospheres which are turned at the proper angle the three pairs of hooks are seen to be placed in such a way that two pairs oppose each other at an angle of 180°, while the other pair is set midway between them on the quadrant. The hooks are about 9 microns in length.

If one has some degree of success in making his preparations some oncospheres will begin to show signs of life. The hooks begin to go through their characteristic motions. So far as I have been able to observe, the opposing hooks usually act in unison, while the third pair alternates with them. More seldom all three pairs of hooks act simultaneously. In action the opposing pairs bring their distal ends into proximity, while their proximal ends approach the periphery. Then the proximal ends move toward each other, while the distal ends are thus pressed outward from the center against the investing membrane and downward from the pole. When this movement is well under way the points of the third pair are brought to a polar position, and then, about the time of the relaxation of the opposing pairs, their points are moved toward the equator. While this alternation of movements is not absolutely regular, there is a certain rhythm about it which is striking.

With the equatorial movement of the two pairs of hooks the oncosphere undergoes a change of form from the somewhat spherical to a broadly pear-like form, the anterior pole being the broader. At the same time the polar diameter is considerably shortened by an active forward movement of the posterior part of the body.

It has been impossible to diagram the phases of these motions satisfactorily. But since the writer has also been successful in watching the movements in the eggs of *Hymenolepis nana* it seems that anyone interested in this point could easily watch the process to his own satisfaction.

INFECTION EXPERIMENTS. A number of infection experiments have been undertaken using *Chironomous larvae,* a favorite food of the secondary host, *Daphnia, Cyclops, Notonecta,* some larvæ of the *Dytiscidae,* tadpoles of *Rana catesbiana,* besides the salamander itself. Thus far all these infection experiments have failed.

That the experiments should fail on the salamander is peculiar, because, as will be shown later, the plerocercus may develop in it. Unfortunately the experiments were carried on under most adverse conditions, when the animals were feeding either not at all or very poorly at best and when but few eggs could be obtained. The physiological conditions of the resting animal are probably inimical to infection.

Schneider (1904) attempted feeding experiments with *Gammarus locusta, Idotea entomon, Phoxinus laevis,* and *Gasterosteus spinachia* with no results. The *Gammarus* died soon after eating of the eggs (possibly from too heavy infection). The *Idotea* and the fish yielded no results. Since, apparently, he examined only livers of the fish, he might have overlooked an infection.

Leuckart (1879-86: 464) reports a plerocercus found by Gruber in *Cyclops serratulus* which he believed to be the larva of *Proteocephalus torulosa* Batsch. From a comparison of his figure, which is drawn to scale, with measurements of *P. torulosa* it seems that there is some foundation for this view.

The plerocercus of *P. filaroides* is even smaller than the one figured by Leuckart; hence it is not beyond a possibility that *Cyclops,* or *Daphnia,* or *Chironomous* larvæ might be intermediate hosts.

Salamanders living under certain conditions are almost always infected with plerocercoids. The first condition for infection in the wild salamander is that he must live in an infected pond—i. e., the tapeworm must be present in some of the salamanders. During the summer of 1908 one pond was found whose salamanders were not infected with either cestodes or plerocercoids. Further data shows that in infected ponds density of salamander population conditions the amount of plerocercoid infection. The heaviest infection also exists in salamanders which have remained larval for a year or more. Thus the element of time increases the chance of infection.

During the summer of 1908 some larval salamanders of the first year were obtained from a Kansas pond. Every salamander opened at that time possessed a moderate infection of cestodes, but no cysts containing plerocercoids were noted; they may have been overlooked. The remaining larvæ were kept in a large aquarium, where they underwent metamorphosis. Some of these were put in small aquarium-jars from time to time, while others were allowed to remain in the large aquarium. They were trained to feed on liver and after a short period of feeding ripe proglottids were passed. When well fed the number of proglottids passed, and hence the number of eggs discharged, was quite large. In the limited quantity of water in the jars a great opportunity for autoinfection through the mouth was offered. Yet, whether the infection with plerocercoids resulted from this period or from an earlier period could not be ascertained with certainty, because no control experiments could be undertaken at that time.

After a period of 4-6 weeks, during which it was possible for infection to occur, the salamanders began to die from some cause not yet ascertained, though a species of *Opalina* was abundant in many that died. These dead animals were found to have a moderate infection with cestodes. Plerocercoids were encysted in all the abdominal viscera and in the muscles of the abdominal wall. The extent of the plerocercoid infection in the first few animals examined was not fully ascertained because of lack of experience in collecting such material and because the significance of the infection was not realized. Later animals had a heavy infection. Cysts have seldom been found in the liver, the organ of heaviest (?) infection according to the other investigators. Cysts were most frequent in the abdominal muscles, less numerous in the submucous layer of the alimentary tract. They have been removed from the spleen, the fat bodies, the mesentery, the ovaries, the testes, the pericardium, and the kidneys. Some plerocercoids have been removed from the abdominal cavity, where they were moving about freely. Furthermore, some plerocercoids have been removed from the lumen of the intestinal tract itself when the host had been in captivity and had fed on a strictly liver diet for three to five months. Plainly no invertebrate host figured in the development of these plerocercoids and in their transfer to the alimentary tract.

The plerocercoids (Fig. 6) from the lumen of the intestine are quite invariably longer than those from cysts and from the abdominal cavity. There is, moreover, a change in the peculiar end-organ, which is much reduced in size in these specimens. Compare Figures 4, 5, 6, 7, 8, which show a series of five specimens, Figure 4 from a cyst, Figure 5 from the abdominal cavity, and Figures 6, 7, 8 from the intestinal tract. A marked reduction in the size of the end-organ is noted in Figures 6 and 7, while in Figure 8 no end-organ is visible. The end-organ in the adult scolex is small (Fig. 23) and may not always be seen in toto mounts.

The finding of these larvæ free in the intestinal tract and free in the abdominal cavity in spite of all precautions to guard against error and after a period of from three to five months of liver feeding, during which the intervention of invertebrate hosts was impossible, hints toward a period of wandering after the plerocercus has gained his development. That a plerocercus can penetrate the submucous and mucous layers of the salamander intestine is not beyond comprehension. Young (1908: 186) considers that the young larvæ of *Taenia serrata,* after they have lost their hooks, may leave the cysts to wander out of the liver. In every host well infected with plerocercoids some cysts must necessarily lie very close to the inner mucous layer of the intestine. In these cases the possibility of the plerocercus reaching the intestinal lumen is not too remote to account for an infrequent infection. Although in one host one plerocercus was found moving freely in a bloody area under the peritoneum and in another host one plerocercus was found in a bloody area in the muscles of the stomach wall, I am not ready to say that an active migration actually occurs. For the most part it appears, until more data is at hand, that the majority of the encysted larvæ are doomed to fail to develop into cestodes. This would be true except in cases of cannibalism, which cases occur only rarely among salamanders. My data seem to hint rather strongly toward direct development, but the possibility and the probability of invertebrate hosts playing a rôle in the infection must not be overlooked. Indeed, even if direct development be eventually proven, the invertebrates are not thereby disproven to act as infective agents.

The discrepancy in size between the end-organ of the plerocercoid from cysts and the end-organ of adult cestodes was so great that it seemed best to determine by further experiments whether this plerocercoid was the larva of our salamander cestodes. Consequently on Oct. 17, 1908, two salamanders known to be uninfected were anesthetized, and each was injected per mouth with 16 cysts. Later one of these animals was put into earth to hibernate, while the other was trained to eat liver. This last one was fed November 13 with 31 plerocercoids embedded in a piece of kidney. On November 29, 42 days after the first infection and 16 days after the second infection, the first ripe proglottids were passed. At this time there were four pieces 10-20 mm. long and 10-12 pieces 2-5 mm. long. The proglottids and eggs were typical for the salamander cestode. Since this time a large number of proglottids have been passed, not all of them being ripe. The host is yet alive, so no idea of the extent of the infection can be given.

At the time of the second infection, November 13, two other salamanders, believed to have a light infection, were fed cysts in pieces of kidney, the larger of the two receiving 30 cysts, the smaller 24 cysts. Since this time these two salamanders have yielded many pieces of unripe cestodes and a few pieces containing ripe proglottids. On Jan. 21, 1909, 69 days after the infection, the smaller specimen died. When examined many plerocercoids were removed from the body, none from the bony cavity, none from the intestine; 32 cestodes were taken from the pyloric end of the intestine. These cestodes were in all particulars like those removed from wild salamanders. This is by far the heaviest infection in salamanders which has come under my observation.

Two days later another salamander died which had come from the same pond and which had been kept in an adjoining aquarium-jar under similar conditions except that it had not been fed plerocercoids. Thus it served as a control animal. This animal had no adult cestodes, but three plerocercoids were removed from the body cavity and three larval cestodes from the lumen of the intestine, besides, of course, the many plerocercoids from the other parts of the body.

These few experiments with feeding plerocercoids furnish conclusive evidence, first, that the encysted plerocercoid is the larval form of the cestode found in the same host; second, that the period of development from the plerocercus after ingestion is short.

The experimental part of the work is necessarily incomplete, but it is the intention of the writer to continue the experiments in the hope that the life history of this genus of cestodes may be fully elucidated.

RELATIONSHIPS OF THE SPECIES. The nearest described species to *Proteocephalus filaroides* is *Proteocephalus Lönnbergii* Fuhrmann, from *Necturus maculatus* Raf., a North American perennibranchiate amphibian. In nearly all its measurements *P. Lönnbergii* exceeds *P. filaroides*, but in their general characteristics they are much alike. Both have the peculiar end-organ, the unsegmented neck, the relatively thin and flat strobila, young proglottids longer than broad. In both cestodes the musculature is relatively weak. The excretory ducts are very similar in their relations to the other organs. The numerous testes are arranged on either side of a free median zone. The organs of the inter-ovarial space have similar relationships. The ovaries of *P. Lönnbergii* are a little more branched than in *P. filaroides*.

These two species are widely separated from *Nematotaenia dispar* Goeze, the only other well-described cestode of amphibia.[3] Thus the cestodes of amphibia divide themselves into two groups, the one, represented by *Nematotaenia dispar,* allies itself with the *Taeniadae* in M. Braun's classification, the other group, represented by *P. Lönnbergii* and *P. filaroides,* allies itself with the family *Proteocephalidae* as true *Proteocephalus* species.

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[3] Leidy (1851) reported a new species of cestode from *Bufo Americanus* which he named *Taenia pulchella* Leidy. His description, which is inadequate for diagnostic purposes, follows:

Taenia pulchella, n. sp.

"White, without any admixture of any other color, variable, usually broadest anteriorly. Head quadrilateral, subclavate, obtusely rounded, broader than the neck. Acetabula circular, cupshaped, lateral and opposite, sessile, protractile. Neck very long, cylindroid. Articuli containing several colorless globules; anteriorly subglobular or transversely oval; posterior moniliform, longitudinally oval, or cylindroid and centrally incrassate.

Measurements.—Longest, 9 inches (228.5 mm.). Articuli commencing to be distinctly separate 4 inches (101.5 mm.) from the head. Breadth anteriorly, 1/4 line (.52 mm.); posteriorly, 1/6 line (.35 mm.); anterior articula, 1/6 line (.35 mm.) long; posterior, 1/4 line (.52 mm.). Acetabula, 1/166 inch (.153 mm.) in diameter. Smallest, 2 inches (50.8 mm.). Head, 1/75 inch (.338 mm.) broad. Articuli commencing distinctly separate 3/4 inch (19.05 mm.) from the head. Broadest part of neck, 1/90 inch (.282 mm.); short distance posterior to the head, 1/125 inch (.203 mm.). Anterior articuli, 1/100 inch (.253 mm.) diameter; posterior, 1/144 inch (.176 mm.) long; 1/200 (.127 mm.) broad at extremities, 1/133 inch (.191 mm.) broad at middle. Acetabula, 1/200 inch (.127 mm.) diameter.

Habitation.—Small intestine of *Bufo Americanus.*

Remarks.—Closely resembles the *Taenia dispar.* Goeze, found in the *Bufo viridis*, etc., but it is relatively longer and is never colored."

It is not possible now to determine whether this be a *Proteocephalus* species or whether it belongs with the *Nematotaenia* or is, in fact, *Nematotaenia dispar.* The latter species has been reported by Stiles and Hassall (1894), and by Wright (1879), from North American species of *Bufo.*

The study of this cestode is necessarily incomplete, yet it is hoped that the facts here presented may prove to be an addition to our knowledge of the genus *Proteocephalus* Weinland, and in particular to our knowledge of those members of the genus inhabiting amphibia.

The work on this form was carried out in the Zoological Laboratory of the University of Nebraska under the direction of Dr. Henry B. Ward. To him my sincere thanks are due for the use of his extensive private library, for the use of material for comparisons, and for his interest and cooperation. I am also indebted to Dr. J. H. Powers for assistance in securing preserved and living material and for his advice in the care of experimental animals.

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EXPLANATION OF PLATES.

All drawings, unless otherwise stated, were drawn with the aid of a camera lucida, and details were added with the same magnification. The magnifications given are approximate.

ABBREVIATIONS.

ci.	Cirrus.	*od.*	Oviduct.
cip.	Cirrus pouch.	*oocp.*	Oöcapt.
cm.	Circular muscles.	*oot.*	Oötype.
cut.	Cuticula.	*ov.*	Ovary.
cvid.	Common vitelline duct.	*rs.*	Receptaculum seminis.
dex.	Dorsal excretory duct.	*sh.*	Shell-gland cell.
eo.	End-organ.	*sm.*	Subcuticular muscles.
ep.	Epithelium.	*t.*	Testis.
fd.	Fat globules.	*up.*	Uterine passage.
glc.	Gland cells.	*ut.*	Uterus.
lm.	Longitudinal muscles.	*va.*	Vagina.
lop.	Lateral uterine outpocketings.	vd.	Vas deferens.
		vef.	Vas efferens.
mrh.	Fibers of muscle rhomboid.	*cer.*	Ventral excretory duct.
mst.	Muscle star.	*vi.*	Vitellaria.
n.	Longitudinal nerve.	*vid.*	Vitelline duct.
nr.	Nerve ring.	*vop.*	Ventral uterine out-pocketings.
nst.	Strands of nuclei.		

PLATE I.

Fig. 1.—Schematic diagram of male genital system from the dorsal side. Reconstruction from camera outlines. × 40.

Fig. 2.—A sexually mature proglottid seen from the ventral surface. From a toto mount. × 55.

Fig. 3.—Diagram of organs of inter-ovarial space. Reconstruction from camera outlines, somewhat simplified by displacing the organs. Ventral side uppermost. × 250.

Fig. 4.—Plerocercoid from a cyst, optical section. The suckers, *bo*, drawn within the body. Note large end organ, *eo.* × 40.

Fig. 5.—Plerocercoid from the body cavity, optical section. × 40.

Fig. 6.—Plerocercoid from intestine, optical section. × 40.

Fig. 7.—Scolex of plerocercoid from intestine, optical section. Note the reduction in size of the end organ. × 40.

Fig. 8.—Scolex of larva from intestine, optical section. No end-organ visible. × 40.

Fig. 9.—Scolex of adult cestode, optical section. × 40.

Fig. 10.—Schematic diagram of the lateral field of proglottid. Redrawn from a camera outline. The dotted circle indicates the area in which the flame cells are most numerous. Anastomosis of the ventral excretory duct, *vexa.* × 130.

Fig. 11.—Diagram similar to Figure 10, showing relation of cirrus, nerve-cord, and excretory vessels. The cirrus passes between the dorsal and ventral excretory ducts. × 130.

PLATE I

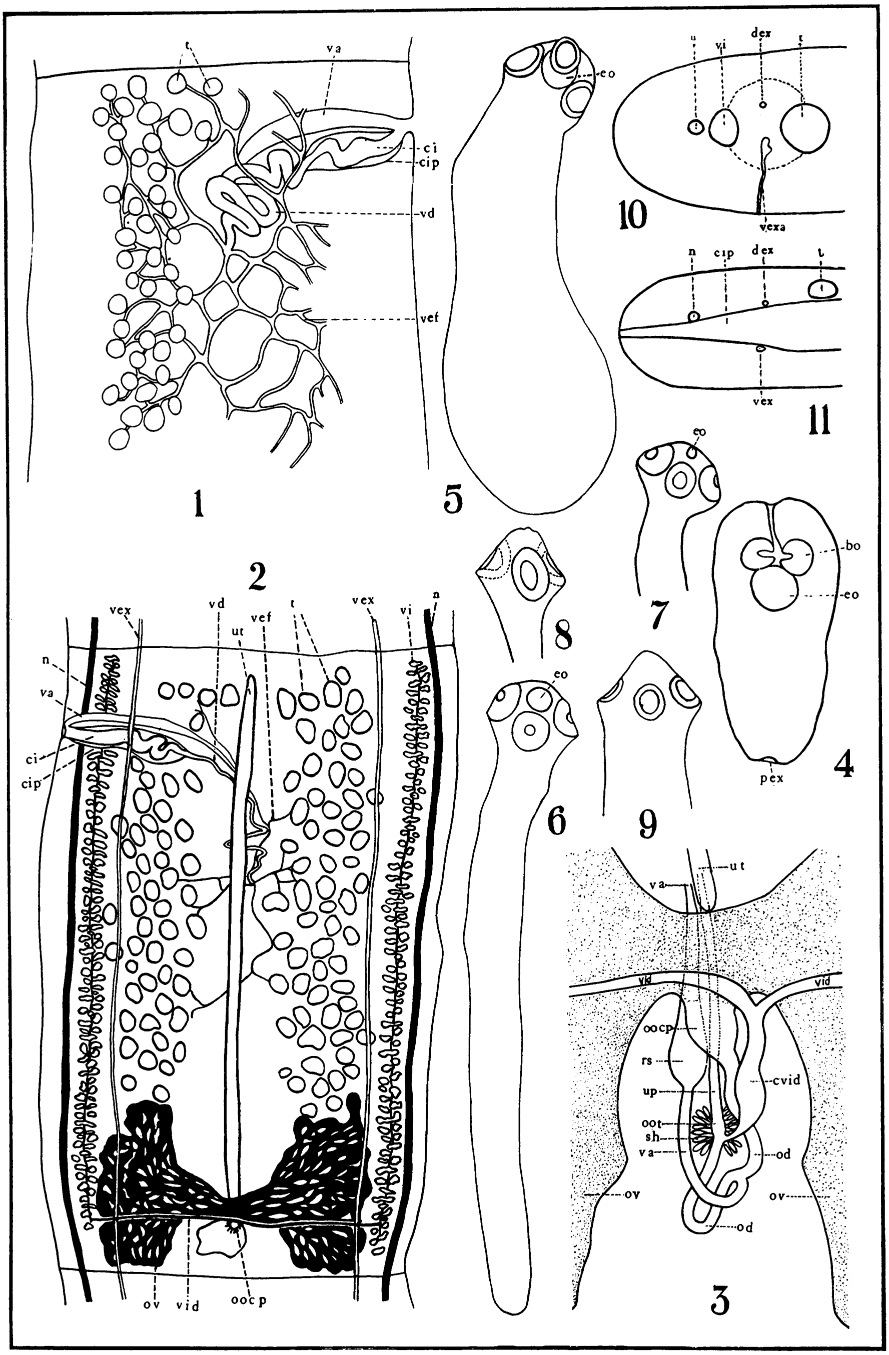
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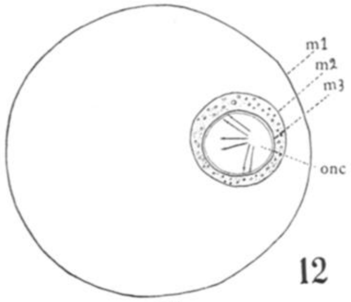
PLATE II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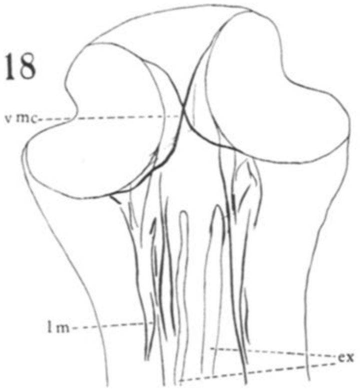
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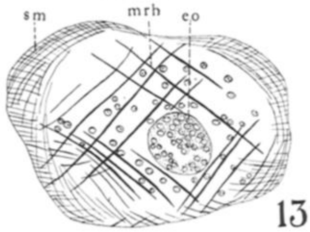
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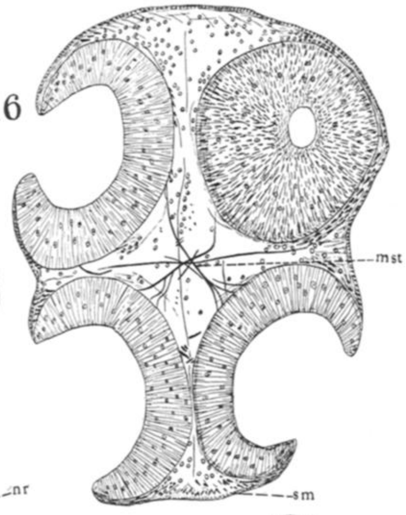
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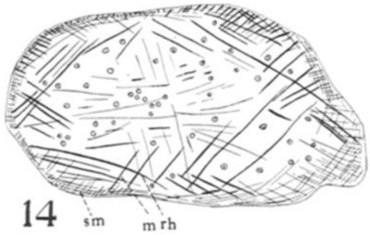
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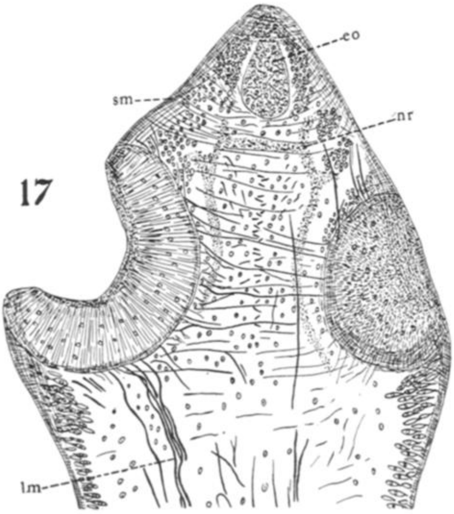
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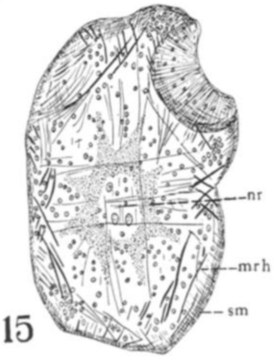
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PLATE II.

Fig. 12.—Egg showing three membranes, *m1, m2 and m3;* also the oncosphere, *onc,* with its six hooks. × 325.

Fig. 13.—Scolex of adult cestode; cross-section showing rhomboid of muscle-fibers, *mrh,* the subcuticular muscles, *sm,* and the end-organ, *eo.* Nuclei are figured in figures 13, 14, 15, 16, 17. × 315.

Fig. 14.—Scolex of adult cestode; cross-section 30-40 microns below tip showing rhomboid of muscle fibers, also weak transverse and dorso-ventral muscle fibers. × 315.

Fig. 15.—Scolex of adult cestode; cross-section 60-70 microns below tip showing nerve-ring, the persisting fibers of the muscle rhomboid, also weak dorso-ventral and transverse muscle fibers. × 195.

Fig. 16.—Scolex of adult cestode; cross-section 220-230 microns below tip, showing muscle star, composed of the horizontal muscle cross and the dorso-ventral and lateral muscle fibers. × 195.

Fig. 17.—Scolex of adult cestode; longitudinal section through opposing suckers. × 195.

Fig. 18.—Scolex of adult cestode; longitudinal section showing vertical muscle cross, *vmc,* between *adjacent* suckers. Two excretory vessels are seen at *ex.* × 195.

PLATE III.

Fig. 19.—Cross-section of proglottid through the region of the oöcapt. Note the vitelline ducts passing ventral to the ventral excretory duct. × 80.

Fig. 20.—Cross-section of vas deferens after distention by spermatozoa. × 315.

Fig. 21.—Vasa deferentia and their anastomoses, showing frequency of nuclei on the delicate membrane. × 315.

Fig. 22.—Vas deferens, proximal end in cross-section. Note the two layers of epithelia. × 315.

Fig. 23.—Head and neck of adult cestode, optical section. Stippled area indicates area of fat globules. Head flattened. × 50.

Fig. 24.—Oöcapt and oviduct. Cubical epithelium bearing cilia, *cep*. Longitudinal section. × 630.

Fig. 25.—Cirrus and vagina from a frontal section of a proglottid. Common genital sinus or atrium, *gsi;* sphincter muscle of vagina, *sphm;* ductus ejaculatorius, *dej;* prostate gland cells, *prgl.*. × 315.

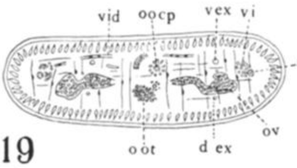
Fig. 26.—Vagina, musculature somewhat idealized. Cross-section. × 630.

Fig. 27.—Uterus and a ventrally directed out-pocketing. From a cross-section. × 315.

Fig. 28.—Uterus from section adjacent to that figured in Figure 27. No ventral out-pocketing. × 315.

Fig. 29.—Uterus and ventral out-pocketing. Note the way in which the ventral wall of the uterus apparently separates the median uterus from the ventral diverticulum. Figures 27, 28 and 29 from the same proglottid delineate about the same stage of uterine development as is shown in Figure 33. × 315.

PLATE III



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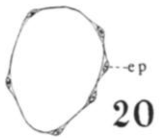

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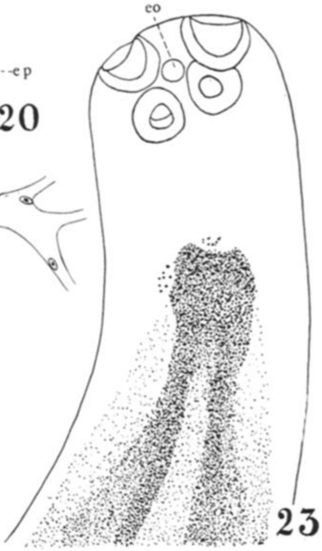

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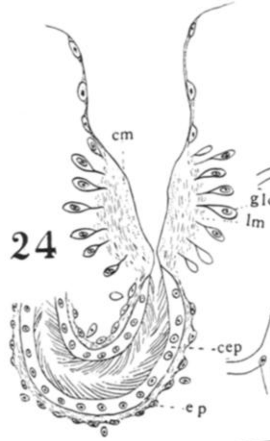

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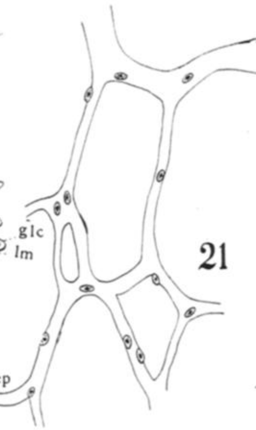

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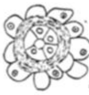

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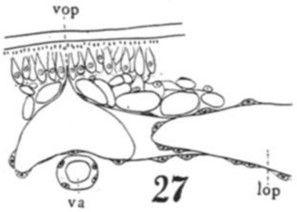

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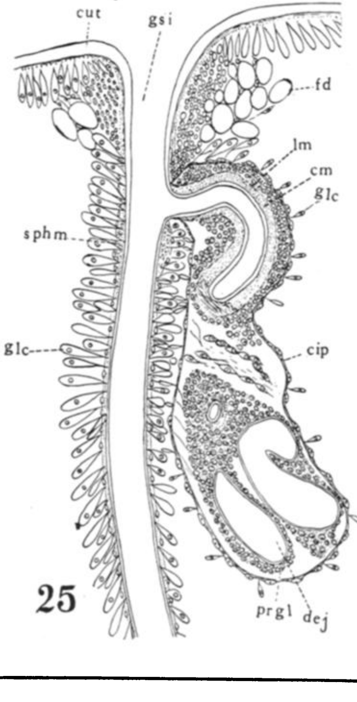

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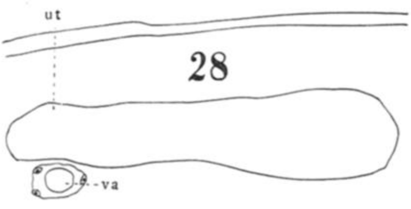

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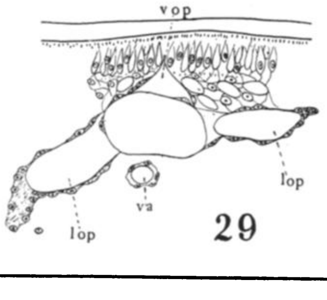

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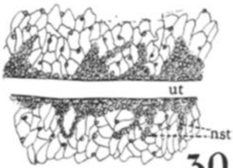
PLATE IV



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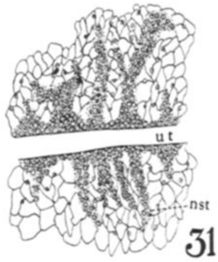

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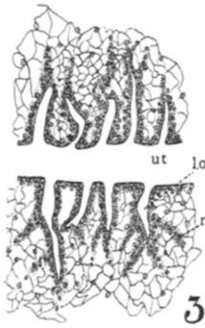

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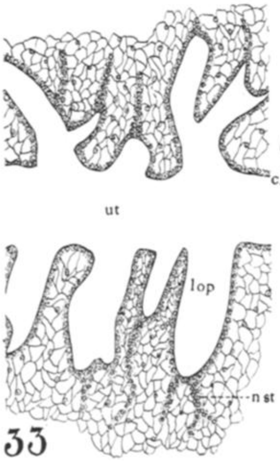

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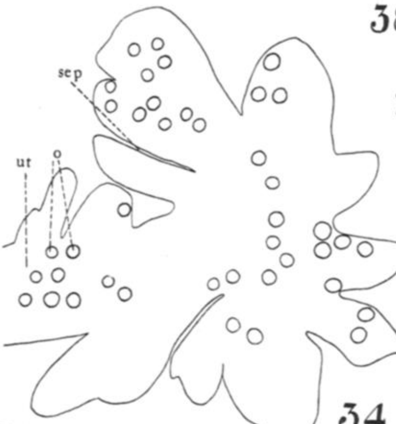

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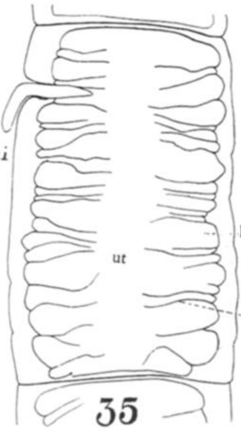

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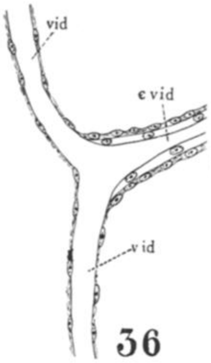

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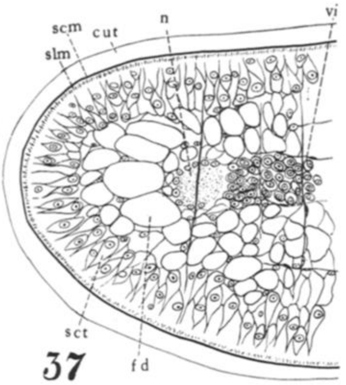

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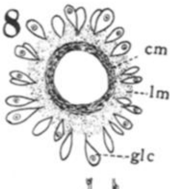

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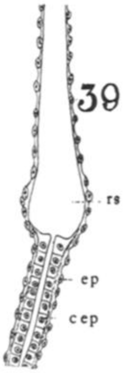

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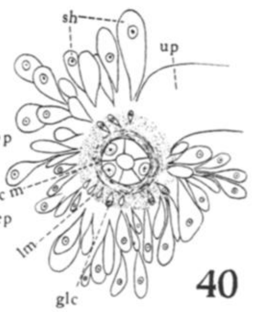

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PLATE IV.

Figs. 30, 31, 32, 33, 34. Stages in the development of the lateral uterine out-pocketings, from a toto mount. Note in Figure 30 the simple strands of nuclei arising from little heaps of cells; in Figure 31 the multiplication of nuclei and the lengthening of the strands; in Figure 32 the appearance of a lumen in the strands, and the strands branching. Note in Figure 33 the broader median uterus and the increased volume of the out-pocketings. Note in Figure 34 the few eggs, *o*, in the uterus, a septum forming at *sep* by the crowding together of the walls of the neighboring diverticula. Nuclei omitted. × 230.

Fig. 35.—Ripe proglottid. Septa, *sep*, between the large lateral diverticula of the uterus. Cirrus evaginated. From a frontal section. × 30.

Fig. 36.—Paired vitelline ducts and the beginning of the common vitelline duct. × 315.

Fig. 37.—Lateral field of a proglottid, cross-section. Note the large oval spaces where the fat globules are located; circular and longitudinal subcuticular muscles, *scm* and *sm;* subcuticular cells, *sct.* × 315.

Fig. 38.—Oôcapt in cross-section. Note the gland cells and the absence of a limiting epithelium. × 630.

Fig. 39.—Lower vagina. Receptaculum seminis, epithelium, cubical epithelium, *cep.* × 315.

Fig. 40.—Oötype and shell-gland with the beginning of the uterine passage in outline; cross-section. × 630.